Functional Anatomy of the Macropodid Pes

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(Communicated by M.L. Augee)

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The functional anatomy of the sthenurine pes was investigated, based on a comparative study of the extant macropodines. Comparisons were made with the possum, koala, and wombat to determine a number of plesiomorphic character states associated with the diprotodontid pes. Dissections were made of the hind limb and pes of a number of extant potoroids and macropodids to determine the functional nature of the actions and insertions of the muscles, as well as the nature of the articulations. A cluster analysis was used to sort a collection of 219 fossilised macropodid calcanea from the Pleistocene Victoria Fossil Cave deposit, Naracoorte southeast South Australia. The morphology of the sthenurine calcanea were compared with *Macropus fuliginosus*. The findings support the previously held view that the sthenurine pes had been selectively modified for its weight bearing function during stand-up browsing. Morphological differences between different sthenurine species suggests that the pedal morphology could be useful in the construction of sthenurine phylogeny.

INTRODUCTION

The aim of this research was to investigate the locomotion of the extinct sthenurine kangaroos (subfamily Sthenurinae) by means of a functional analysis of their pes (hindfoot). The locomotory adaptations of the extinct sthenurines may be inferred from a study of modern functional analogues, in this case the macropodines. The structure and function of many aspects of the macropodine pes have been examined to varying degrees in past studies (Parsons 1896; Windle and Parsons 1897; Barnett 1970; Lewis 1964, 1983; and Hopwood and Butterfield 1990). Neither the form of the macropodine pes, nor that of any other animal, is dictated solely by its functional role. Form may be influenced as much by ancestry as by functional adaptations. Unravelling these interactions is an essential aspect of functional analysis. In this case it was necessary to determine what specific features made the pes macropodine (the derived or apomorphic conditions) as opposed to diprotodontid (ancestral or plesiomorphic conditions). All diprotodont marsupials, which include the Macropodidae, share the same basic foot pattern in which the IVth digit is enlarged, sometimes equalling in size, but usually larger than the Vth digit. The Vth digit is in turn larger than the syndactylous IInd and IIIrd digits, which are again larger than the often vestigial or absent hallux or I^{st} digit. This is expressed as the digital formula, IV>V>III=II>I .

At the basis of the concept of modern functional analogues, is the well studied conception of function being reliant on form (Bock and von Wahlert 1965; Gould and Lewontin 1979; Bock 1980, 1981, 1988, 1989; Lauder 1981; Arnold 1983; Gans 1988; Lauder 1990; and Losos 1990). The same authors have expressed the need to use careful consideration of all aspects of the evolution of form when ascribing particular traits to a specific function.

To ascertain the plesiomorphic diprotodontid pes structure from which the

macropodine pes has evolved, it was necessary to examine the characteristics of several different marsupial families. Evidence from studies of craniodental characters place the Macropodidae close to, but derived from, the Potoroidae. Together these two are closely related to, but derived from, the Phalangerids (possums), (Dollo 1899, Bensley 1903, Raven and Gregory 1946, Archer 1984, and Flannery 1983). The superfamily Macropodoidea is broken up into two main families, the Macropodidae and Potoroidae.

The muscular anatomy of the hindlimb and pes of the macropodines has previously been examined by Parsons (1896), Windle and Parsons (1897), Craven (1971), Adnams-Hodges (1988), and most recently and comprehensively by Hopwood and Butterfield (1990). Only Parsons (1896) and Lewis (1983) have investigated the anatomy of the binding ligaments of the pes. The osteological remains of the macropodine foot and the nature of the articulations have also been dealt with to various degrees by Owen (1875); Parsons (1896); Windle and Parsons (1897); Barnett (1970); Lewis (1964, 1983); and Hopwood and Butterfield (1990).

The locomotion of the macropodids, initially documented by Muybridge (1887) has been well studied, particularly by Badaux (1965), Windsor and Dagg (1971), Marshall (1974), Bennett (1987), Biewener and Blickhan (1988), and Baudinette (1994). Macropodines progress by a ricochetal saltatory mode of locomotion, where both of the hind-feet are placed on the ground simultaneously. Weight is transmitted through the tibia to the astragalus, the calcaneum, through the cuboid, then through to the elongated fourth metatarsal. Windsor and Dagg (1971) in their study of nineteen macropodine species were able to identify four gaits: 1) the slow progression - pentapedal (four limbs and tail), used mainly during grazing; 2) the walk - the pairs of the limbs are asynchronously placed in contact with the substrate, and expressed only in *Dendrolagus* the tree kangaroo; 3) the quadrupedal bound - the use of the hind feet followed by the forefeet, exhibited only in *Setonix*, *Dendrolagus*, *Petrogale* and the Potoroidae; 4) the bipedal hop - he fastest gait, with synchronous placement of the hind feet on the ground.

Independent studies by Marshall (1974), and previously Badaux (1965), characterised macropodine locomotion as hopping or bipedal ricochetal saltation, where the hind feet are synchronously placed in contact with the ground. Despite macropodines possessing at least four gaits, it seems that the general elongated form of the macropodine locomotor apparatus has been modified primarily in relation to the fastest gait, the bipedal hop. This is supported by evidence associated with the energetic efficiency of this gait at high speeds (Dawson and Taylor 1973, Alexander and Vernon 1975, Cavagna et al. 1977, Baudinette et. al. 1992, Baudinette 1994), which can be primarily explained by the physical return of stored energy in the hindlimb (Alexander and Vernon 1975, Alexander 1984, and Bennett and Taylor 1995).

Based on a study of cranial and dental characters, Raven and Gregory (1946) examined the adaptive branching of the kangaroos and its relation to habitat. The pes can also be used in a similar function as eluded to by Windsor and Dagg (1971). The macropodines have diversified to occupy a wide variety of habitats ranging from open plains (*Macropus rufus*) to tree top canopies (*Dendrolagus*). An examination of the varied pedal morphology of the macropodines from segregated habitats should provide an excellent source of definition for the functional nature of the derived features.

Wells and Tedford (1995) noted some major differences between the sthenurine kangaroos, and the extant (modern) macropodines. The first major difference is in the generally bulkier nature of the animal; the skull and teeth being adapted for tough feed browsing, rather than grazing which predominates in the modern macropodines. The structure of the shoulder facilitated raising the arms above the head, with the associated long digits of the manus (hand) enabling it to reach higher foliage. Structure of the spine and tail vertebrae suggest adaptations to standing upright, also for procuring food. These authors also note that the hindfeet are functionally one-toed or monodactylous, with further reduction of the second, third, and fifth digits differing from the modern generalised macropodine form.

MATERIALS AND METHODS

All of the fossil bones used in this study were excavated from the "Victoria Fossil cave" at Naracoorte from 1972 to the 1988. Measurements were also taken on various reference skeletons from extant species in Flinders University and South Australian Museum collections. The specimens are listed in Table 1.

TABLE 1

The reference skeletons examined from the South Australia Museum (M) and Flinders University Reseacrh (FUR) collections.

Specimen		Reference
POTOROIDAE	*Hypsiprymnodon moschatus*	M11940
	Aepyprymnus rufescens	FUR
	Bettongia lesseur	FUR 011
	Bettongia penicillata	M8286
MACROPODIDAE	*Macropus fuliginosus*	FUR
	Macropus rufus	FUR 001
	Macropus eugenii	FU 010
	Macropus rufogriseus	M16370
	Macropus greyi	M2121
	Macropus parma	M7191
	Macropus irma	M16489
	Macropus robustus	M3695
	Macropus parryi	M14103
	Macropus dorsalis	M7967
	Dorcopsis sp.	M13754
	Petrogale lateralis	M12555
	Setonix brachyurus	M14102
	Wallabia bicolor	M16469
	Dendrolagus bennettianus	M5530
PHALANGERIDAE	*Pseudochirus peregrinus*	FUR 004
VOMBATIDAE	*Lasiorhinus latifrons*	FUR 006
PHASCOLARCTIDAE	Phascolarctos cinereus	FUR 009

Muscles, tendons and ligaments

The hind limbs were removed from a number of kangaroo carcasses for the purpose of dissection. Whole frozen specimens of one female western grey (*M. fuliginosus*) and one female red kangaroo (*Macropus rufus*) were provided by the South Australian

National Parks and Wildlife Service. One Tammar wallaby (*Macropus eugenii*), one bur-
rowing bettong (*Bettongia lesueur*) and one rufous bettong (*Aepyprymnus rufescens*)
from the frozen specimen collection at Flinders University were dissected.

All specimens had been frozen soon after death and stored in a freezer room held
at -15°C. Two to three days prior to their dissection they were transferred to a refrigerat-
ed room held at 4°C. The specimens remained in the refrigerated room for the duration,
to minimise deterioration of the flesh. All dissections were carried out using a standard
dissection kit. After all of the flesh was dissected away the limbs of the specimens were
macerated, cleaned and bleached so that they could be illustrated and examined for mus-
cle and ligament scars.

The measurements taken on the calcaneum are displayed in Fig. 1. The terms used
to describe the features of the pes follows Murray (1995). Figure 2 shows the anatomical
terms used in the descriptive anatomy.

Statistical analysis

Twelve measurements were made on the calcanea of both the extinct and extant
taxa. A cluster analysis was performed on this data matrix to determine the natural
groupings of the specimens measured.

The statistical program SPSS (1989) was used to cluster the fossil bones into nat-
ural groupings based on the measurements taken. Recognition of the distribution pat-
terns of operational taxonomic units (OTU) and groups of OTU's (taxa) were carried
out in a hyper dimensional (12 dimensions) space (phenetic A space), where a pattern
is any discernible property of the distribution and groups of OTU's in A space. I have
chosen a cosine measure of similarity. The use of cosine as a similarity measurement is
particularly useful in the measurement of shape (Sneath and Sokal 1973). This stan-
dardises size so that measurement of similarity is on shape only. The agglomerative
clustering technique was used to cluster the OTU's and is the most widely accepted
and tested method. There are several methods available to group the specimens, how-
ever the most widely accepted, and also default setting for the SPSS program, is the
sequential, agglomerative, hierarchical, non-overlapping clustering method (SAHN).

To summarise the differences, a principal component analysis was carried out on
the same data set. Principle components analysis measures the variance for the entire
group and then displays the variance in the form of major components.

RESULTS

Comparative Anatomy and Cladistic Analysis of the Marsupial Pes (Tables 2-4)

Anatomy of the crus and pes of the western grey kangaroo, Macropus fuliginosus

Osteology

Separate bones of the crus and pes include: tibia, fibula, seven tarsal bones, four
metatarsals, twelve phalanges, a plantar sesamoid, four metatarsophalangeal sesamoids
(Figs 3 and 4).

i) The crus: (between knee and ankle) comprising of tibia and fibula: On the tibia
the condyles are located on the posterior half of the head of the tibia. The tibia articulates
with the fibula along the posterolateral aspect of the lateral condyle of the tibia. The tibia
is greatly expanded anteroposteriorly compared with its transverse width. Proximally the
tibia is expanded, with the shaft roughly triangular in cross section as described by Owen
(1874–77). Distally the shaft is circular to ovoid at its extremity, expanding into the
medial malleolus. The proximal lateral surface of the shaft is deeply concave to receive
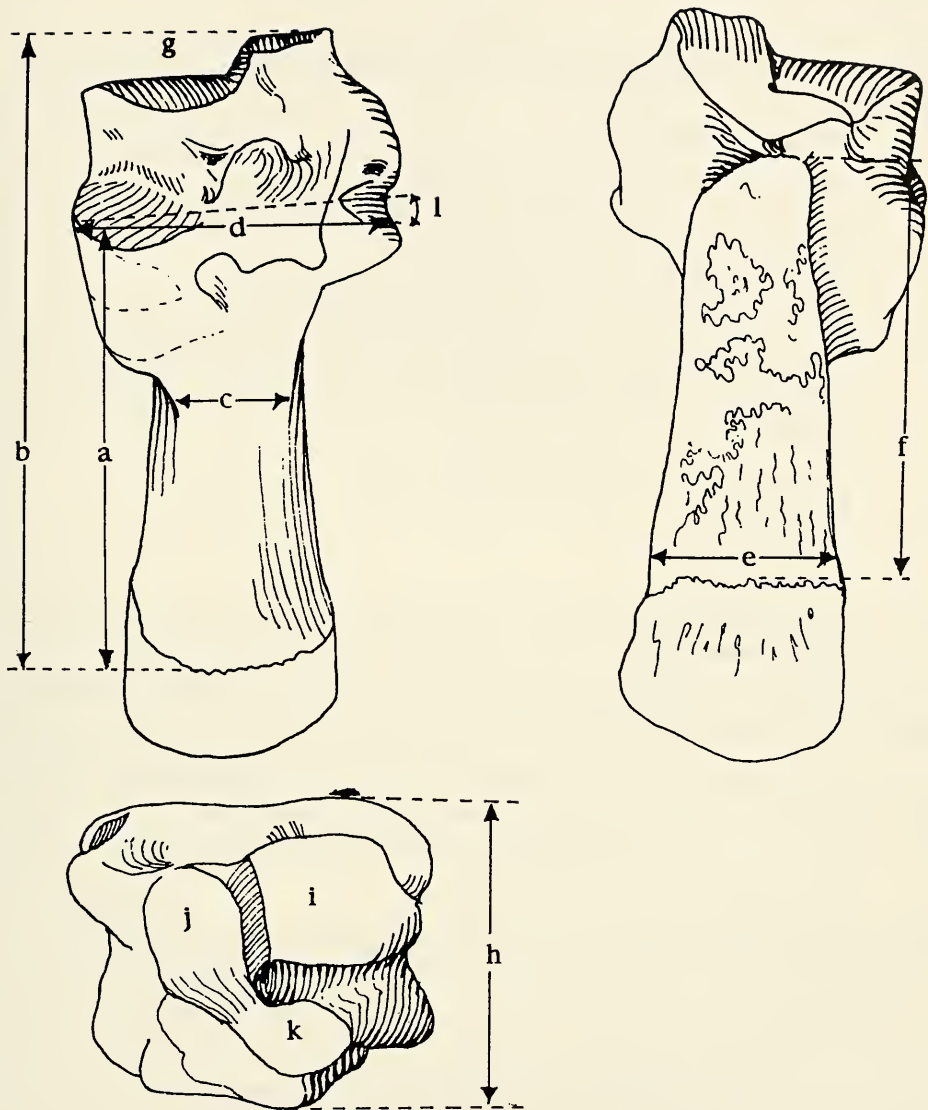the extensor muscle mass of the crus.

Figure 1. a-The length of the calcaneum from the epiphysial junction to the line of transverse axis of the astragalus: b- The length of the calcaneum from the epiphysial articulation to the distal portion of the dorsolateral cuboid facet on the calcaneum: c- The width of the dorsal portion of the tuber calcanei of the calcaneum measured transversely at the posterior region of the lateral process and the posterior region of the sustentaculum tali: d- Width across the pivot point, or line of transverse axis of the astragalus: e- The width of the plantar surface of the calcaneum measured at the most posterior aspect of the tuber calcanei, not including the epiphysis if present: f- Plantar surface length, measured from the epiphysial arthrosis on the plantar surface to the transverse plantar sulcus on the calcaneum or when not present, to the distal portion of the plantar tuberosity on the calcaneum: g- The prominence of the dorsolateral cuboid facet on the calcaneum, measured from the face of the dorsomedial cuboid facet on the calcaneum to the most distal portion of the dorsolateral cuboid facet on the calcaneum: h- The height of the calcaneum measured dorsoventrally at the most posterior aspect of the tuber calcanei, not including the epiphysis if present: i- The surface area of the dorsomedial cuboid facet on the calcaneum: j- The surface area of the dorsolateral cuboid facet on the calcaneum: k- The surface area of the ventromedian cuboid facet on the calcaneum: l- The angle of transverse axis of the astragalus measured from the central axis of the calcaneum.

TABLE 2

The characters which were determined to be plesiomorphic.

Character	State
1	Weak and asymmetrical ridges
2	Malleolar fossa is situated posteromedially, and not distinct
3	The medial trochlear crest is greater in length than the lateral trochlear crest
4	Large scar for the posterior talocalcaneal ligament
5	Long astragalar head and neck with no distinct notch for the trochlear bursa
6	The lateral trochlear crest is aligned with the lateral border of the navicular facet on the astragalus
7	The medial trochlear crest aligns with the lateral border of the navicular facet on the astragalus
8	The navicular facet is broad, with its longitudinal axis transecting the lateral trochlear crest of the astragalus
9	Transversely wide sustentaculum tali which tapers medially
10	Uninformative
11	The sustentaculum tali is deflected anteromedially, and the base of the sustentaculum tali is rounded posteriorly
12	The articular surface for the astragalus on the calcaneum is continuous transversely, and shallowly convex anteroposteriorly
13	The lateral facet for the astragalus on the calcaneum is higher than the medial facet for the astragalus

Derived characters of other diprotodontids:

5	The wombat possesses both a long astragalar head and neck and a small notch for the trochlear bursa
11	In the koala, the base of the sustentaculum tali is straight, nearly horizontal
14	Single smooth surface distally for articulation with the cuboid in other diprotodontids
15	No transverse plantar sulcus in other diprotodontids
16 & 17	Single articulating surface for the cuboid in other diprotodontids

TABLE 3

The shared derived characters of Hypsiprymnodon and Macropus.

Character	State
1	The trochlear ridges are symmetrical and well rounded
6	The lateral trochlear crest is aligned with the lateral portion of the dorsolateral facet (of the calcaneum) when the astragalus is articulated
7	The medial trochlear crest aligns with the median portion of the navicular facet on the astragalus
9	Comparatively transversely narrow astragalus
14	The dorsomedial and dorsolateral facets (for the cuboid) are equal in height in distal aspect
16	Presence of a groove separating the dorsomedial and ventromedian facets (for the cuboid) on the calcaneum

TABLE 4

The derived or apomorphic characters of the generalised macropodine pes.

Character	State
2	There is a distinct notch on the transversely wider medial malleolar fossa
3	The parallel trochlear ridges are angled more obliquely
4	The scar for the posterior talocalcaneal ligament is much reduced
5	The development of a distinct notch for the trochlear bursa
8	The navicular facet is broader, and its longitudinal axis transects the medial trochlear crest
10	The tuber calcanei is relatively narrow and elongated anteroposteriorly
11	The sustentaculum tali is deflected anteromedially, and curved posteroventrally
12	There are two separate lobate facets (on the calcaneum) for articulation with the astragalus
13	The medial and lateral facets (for the astragalus) on the calcaneum are equal in height
15	The transverse plantar sulcus is anteroposteriorly narrow
17	The cuboidocalcaneal step is short but distinct

The fibula

is a long and slender bone, with the head being the most expanded part, anteropos-
teriorly. It articulates with the transverse fibular groove on the posterolateral aspect of
the tibia. The fibula shaft is thickest proximally, with the lateral surface, convex and the
medial surface concave to articulate with the lateral aspect of the tibia, as well as provid-
ing area for muscle insertion in proximal region. The distal epiphysis is expanded into
the lateral malleolus (Hopwood and Butterfield 1990).

ii) The Pes consists of a number of separate bones: The tarsus consists of seven
separate tarsal bones plus one sesamoid (Hopwood and Butterfield 1990): calcaneum,
astragalus (talus), and Metatarsal IV make up the bulk of the tarsus.

The astragalus

(talus) bears a large articulation dorsally with the distal end of the tibia. The bone
is subdepressed and triangular , with the base turned forward (Owen 1874–77). In medial
or lateral view it is arched, convex dorsally. The dorsal surface is formed mainly by the
trochlear articulation with the tibia, which is convex anteroposteriorly and concave trans-
versely. Further, the dorsal surface is divided into medial and lateral portions by the
respective medial and lateral trochlear grooves, providing facets for the lateral and medi-
al malleoli. Ventrally the astragalus is concave anteroposteriorly, forming the articular
surface for the calcaneum. It is divided into a lateral and medial articulation site, corre-
sponding to articulation sites on the calcaneum. The lateral surface of the head of the
astragalus also articulates with a small area on the dorso medial portion of the calca-
neum. Distally, the astragalus articulates with the navicular bone as well as a small area
on the posteromedial portion of the cuboid.

The calcaneum

articulates dorsomedially with the astragalus, dorsolaterally with the fibula, and
distally with the cuboid. There is a roughened flat surface on the plantar aspect for the
insertion of the large plantar calcaneo cuboid ligament. The calcaneum is roughly trian-
gular in cross section, flattened and broad plantarly. The dorsal surface of the tuber cal-
canei has a smooth surface with a relatively narrow longitudinal ridge extending posteri-
orly. The sustentaculum tali is narrow transversely but deep dorsoplantarly, and is curved
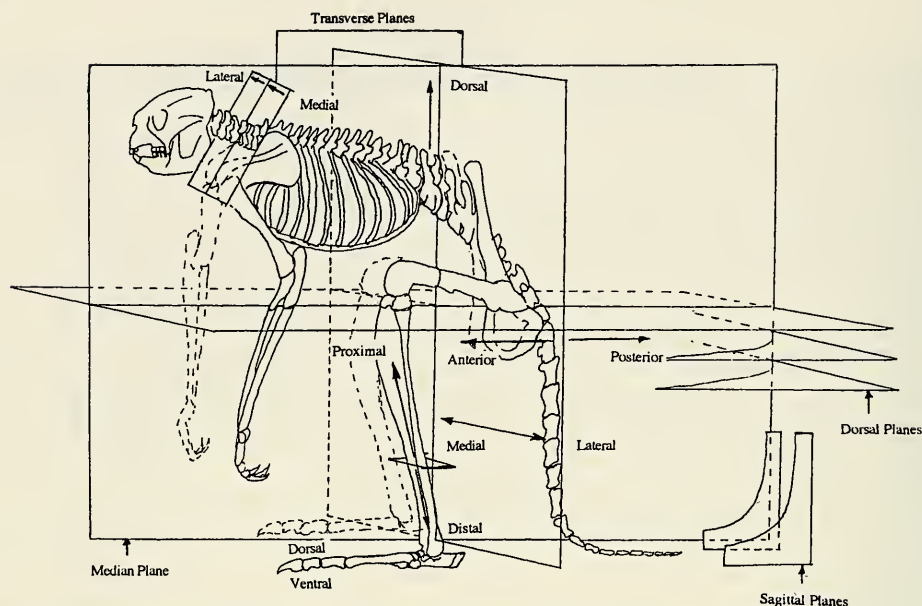
Figure 2. Shows the anatomical and directional terms and planes of the body (Adapted from Leach, 1993)

posteriorly through plantarly. It bears a groove for the flexor digitorum longus. Laterally, the fibular condyle bears an articular facet for the lateral malleolus of the fibula on its posterolateral aspect. Dorsally, the lateral facet for the astragalus is high and rounded, proportioned equally transversely and anteroposteriorly. It is separated from the concave medial facet by a small longitudinal ridge. The ridge of the medial facet sits slightly higher and more anterior to the posterior border of the lateral facet. The fossa for the anterior proximal process of the astragalus is shallow and semicircular. There is a small triangular facet on the dorsomedial aspect of the calcaneum for articulation with the lateral aspect of the neck of the astragalus. Distally, the surface of the dorsomedial facet is transversely broad, rectangular and strongly convex dorsoplantarly. The dorsolateral facet is narrow transversely, but longer dorsoplantarly and narrowing plantarly. This facet is stepped and protrudes more anteriorly than the dorsomedial facet. Ventrally, the dorsolateral facet merges into the ventro median facet, which is of similar size to latter, but broader transversely than dorsoplantarly, and is of sub triangular shape, but with the most plantar aspect not contributing to the plantar surface.

The navicular,
        proximally, is concave, articulating with the corresponding convex head of the astragalus. Laterally, it articulates with the medial surface of the cuboid. It is convex and articulates distally with the entocuneiform and ectocuneiform.

The entocuneiform
        articulates proximally with the navicular, distally with the IInd metatarsal and mesocuneiform, laterally with the cuboid, and medially with the ectocuneiform (Hopwood and Butterfield 1990).

The mesocuneiform
        articulates proximally with the ectocuneiform, distally with the IInd metatarsal, dorsally with the IIIrd metatarsal, and is the smallest tarsal bone.
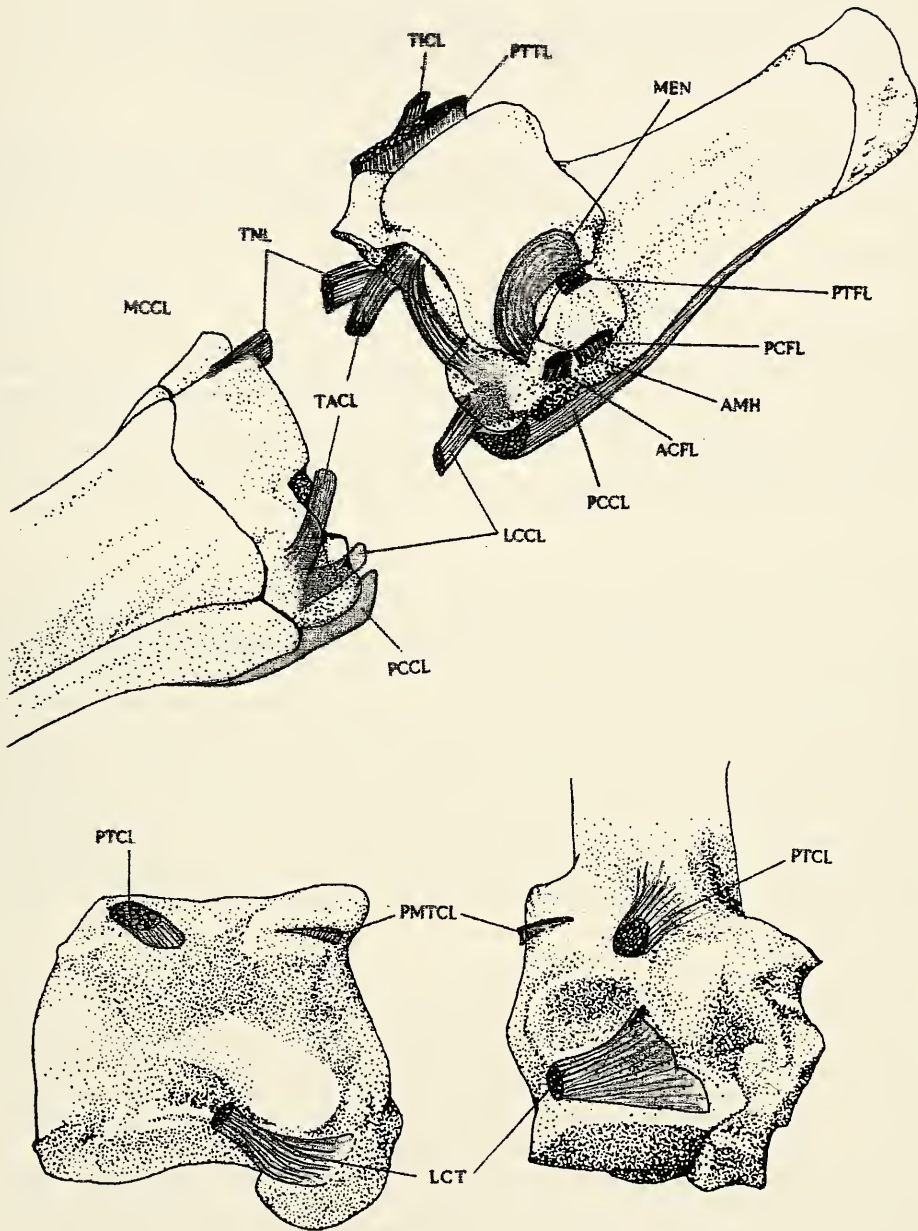
Figure 3. View of the ligaments of the left pes of *Macropus fuliginosus* . **TCL-** tibiocalcaneal ligament ;
PTTL- posterior tibiotalar ligament ; **MEN-** meniscus ; **PTFL-** posterior talofibular ligament ; **PCFL-** posteri-
or calcaneofibular ligament ; **ACFL-** anterior calcaneofibular ligament ; **AHM-** anterior horn of the meniscus ;
PCCL- plantar calcaneocuboid ligament ; **LCCL-** lateral calcaneocuboid ligament ; **MCCL-** medial calca-
neocuboid ligament ; **TNL-** talonavicular ligament ; **TCL-** talocuboid ligament ; **PTCL-** posterior talocalcaneal
ligament ; **PMTCL-** posteromedial talocalcaneal ligament ; **LCT-** ligamentum cervicis tali.

The ectocuneiform

articulates proximally with the navicular, distally with the mesocuneiform and IIIrd metatarsal, medially with the entocuneiform, and laterally with the cuboid and IVth metatarsal, extending backward, beyond and overlapping the entocuneiform (Owen 1874–77).

The cuboid

articulates proximally with the calcaneum accommodating its three facets, distally with IVth and Vth metatarsals, and medially with the navicular and ectocuneiform.

Metatarsal I

Absent

Metatarsal II and III

Metatarsal II articulates proximally with entocuneiform and mesocuneiform, and distally with the first phalanx of digit II. Metatarsal III articulates proximally with meso-cuneiform and entocuneiform, and distally with the first phalanx of digit III. Both metatarsals II and III are reduced greatly in width but not in length. In the middle of the tarsus both lie on the plantar aspect of metatarsal IV, then curve dorsomedially in the distal portion of the metatarsus (Hopwood and Butterfield 1990).

Metatarsal IV

articulates proximally with the cuboid, and proximomedially with the ecto-cuneiform. It articulates medially with metatarsal III, laterally with metatarsal V, and plantarly with the tarsal sesamoid bone (Hopwood and Butterfield 1990). Distally metatarsal IV articulates with the first phalanx of digit IV and the medial and lateral metatarsophalangeal sesamoid bones. The dorsal surface is convex transversely, most so at the most proximal part where it articulates with the cuboid. The plantar surface is slightly concave transversely, mainly in the distal two thirds, but with a deep tuberous keel proximally present as a thick ridge. The proximal plantar surface also provides a site for the attachment of the plantar sesamoid, which is grooved for accommodation of the flexor digitorum longus tendon. The distal articulation is convex dorsoplantarly but nearly flat transversely. Ventrally on the distal articular surface is a median ridge form-ing two concave surfaces for the trochlear articulation of the first phalanx of the metatarsal IV.

Metatarsal V

articulates proximally with the cuboid, and medially with the lateral surface of metatarsal IV. It articulates distally with the first phalanx of digit V and also plantarly with the metatarsophalangeal sesamoid bones of digit V. A significant portion of metatarsal V is in contact with the ground. Proximally this bone possesses a sigmoidal shape, curving up most proximally at its articulation with the cuboid. The rest of the bone is curved in the opposite direction, very greatly curved concavely. Proximally the bone is roughly triangular in cross section. The lower border is thicker than the upper, and primarily in the proximal portion. In plantar aspect metatarsal V is also curved out laterally so that the distal end of this bone lies ventrolaterally to metatarsal IV. The distal articulation with the first phalanx of digit V is convex dorsoplantarly.

Digits

There are three digits corresponding to each of the metatarsals, and the size of these digits conforms well with the size of the metatarsal carrying that digit. The metatarsal IV is the longest digit with the distal digits of metatarsal V extends as far as the articulation between the first and second digits of metatarsal IV.

The ligaments of the pes

In the majority of mammals including humans, the ankle consists of only one joint. It is noted that in macropods the ankle has been modelled into two ankles (Lewis 1980). The first joint is considered the articulation of the tibia with the astragalus and the fibula with the calcaneum, with the second joint (sub talar) being formed between the astragalus and the calcaneum. The *Nomina Anatomica* text suggests that the ankle joint is the talocruralis, i.e. the joint between the tibia and the astragalus. While this joint exists in the macropods, the fibula also articulates with the calcaneum. The articulation of the tibia on the astragalus is a "hinge-like" trochlear joint convergent in form and function with the eutherians (Lewis 1980).

i) Articulatio tarsocruralis (tibiotalar/calcaneofibular) (see Fig. 3): The broader lateral part of the tibial surface articulates directly with the large trochlear groove on the astragalus. This area is separated from the medial articulation by the medial trochlear ridge. The well defined astragalar depression accommodates the terminal articular knob on the tibia. The lateral trochlear ridge separates the trochlear groove from the lateral surface of the astragalus where the medial surface of the fibula articulates.

Medially, there is a ligamentous wall, common to congruent joints. The posterior tibiotalar ligament arises from a long ridge, extending longitudinally on posteromedial aspect of the astragalus. More superficial to this and crossing over the tibiotalar ligament, is the tibiocalcaneal ligament which passes down to attach to the tuberosity on the sustentaculum tali. This is in close proximity to the talo-navicular ligament passing from the medial aspect of the neck of the astragalus to a dorso-lateral position on the navicular. A small cartilaginous meniscus intervenes on this surface in between the fibula and the astragalus, but does not extend up in between the tibia and fibula (Lewis 1980).

Anteriorly, the meniscus continues forward between the fibula and the astragalus, terminating as a fibrous horn, and recurves to attach to the calcaneum. Passing from the fibula to the astragalus, protruding from underneath the meniscus is the posterior talofibular ligament which intervenes between the fibula and the exposed projection of the articular facet on the calcaneum. Also protruding from the astragalus near the astragalar neck, the talocuboid ligament divides into two components; one band transversely forming a strap through which the tendons of the flexor muscles pass, and another band over the cuboid to insert into its lateral surface, where it shares its insertion with a small lateral calcaneocuboid ligament. As with the medial side of the tibia, two ligaments, the posterior and anterior ligaments, cross and bind the fibula and calcaneum, both with origins on the lateral projection of the calcaneum and insertions on their respective diagonally opposite anterior and posterior regions on the distal end of the fibula. On the plantar surface there are two main ligaments binding the calcaneum to the more distal tarsals and metatarsals (Lewis 1980). Crossing from the medial side posteriorly on the calcaneum to an insertion into the cuboid and base of metatarsal IV and V on the ventro-lateral aspect is the large plantar calcaneocuboid ligament. Medially is a comparatively smaller calcaneocuboid ligament originating in the base of the sustentaculum tali and passing to an insertion into the navicular, cuneiform bones and metatarsal II and III.

ii) Talocalcaneocentralis (subtalar joint): This is comprised of the articulation of the astragalus on the medial portion of the calcaneum. There are two main articulating surfaces on the plantar aspect of the astragalus corresponding to the lateral and medial articulating surfaces on the calcaneum. Both surfaces have a predominantly transverse axis, are concave on the astragalus and are convex on the calcaneum (Lewis 1980).

Two main ligaments tightly bind the astragalus to the calcaneum, the anterior and posterior talocalcaneal ligaments. The anterior talocalcaneal ligament is the homologue of the ancestral ligamentum cervicis tali. It extends from the neck of the astragalus to a large insertion into the median portion of the calcaneum (Lewis 1983). The large posterior talocalcaneal ligament extends from a large area of insertion on the astragalus to a similar sized tuberosity in the posterolateral region of the articulating part of the calca-

neum. There is also a small ligament extending between the postero-medial process of the astragalus to the corresponding postero-medial area on the calcaneum. This ligament is not described in any text, and is probably a second fascia of the main posterior talocalcaneal ligament. Similar remodelling of the subtalar joint such as seen in macropods can also be found in the precursors of the artiodactyls (Lewis 1983).

The muscles and tendons of the crus and pes of the western grey kangaroo, *Macropus fuliginosus*

The complete descriptions of the muscles of the crus of the eastern grey (*Macropus giganteus*) have been succinctly described in a previous study, (Hopwood and Butterfield 1990) and will not be dealt with here.

Comparative morphology of modern Macropodines

The muscles and tendons of the hindlimb and pes

The muscles and ligaments of a number of modern macropodid and potoroid forms were examined to determine whether there were any differences in the origins and particularly insertions of the muscles, and to see whether these differed significantly from the form of *M. fuliginosus*. The insertion sites of the tendons did not vary between the different macropod species examined in this study. It was noted however that there was a correlation between the size of the tendon entering an insertion site and the size of the resulting scar.

The comparative osteology of *Macropus fuliginosus*, *Macropus rufus*, and *Dendrolagus bennettianus*

To ascertain some of the features which may be related to habitat in the modern kangaroos, I have chosen to describe two species from two different habitats using *Macropus fuliginosus* as a comparative model.

i) Comparative anatomy of the astragalus: Dorsally in *Dendrolagus bennettianus* the astragalus is subdepressed and rectangular in form, greater transversely than anteroposteriorly, compared with *M. fuliginosus* which is slightly more triangular in form, due largely to the angle of the lateral trochlear crest. *Macropus rufus* is the most triangular of the three specimens with the medial trochlear crest greatly elongated posteriorly. The dorsal surface of the astragalus in the three specimens is formed mainly by the trochlear-like articulation with the tibia. The dorsal surface is divided into three portions by the two-medial and lateral trochlear crests providing facets for the lateral and medial malleoli. The astragali of the specimens are curved convexly anteroposteriorly, greatest in Dendrolagus and least curved in *M. rufus* in keeping with the proportions of the relative calcanea. The trochlear of the astragalus is also curved concavely transversely, deepest in *Dendrolagus* and most shallow in *M. rufus* compared with *M. fuliginosus*. The comparative height of the medial and lateral trochlear crests varies between the three specimens. In *M. fuliginosus* and *M. rufus* the medial trochlear ridge is higher than the lateral trochlear ridge viewed in distal aspect, compared with *D.bennettianus* where these ridges are equal in height.

Ventrally the astragalus is concave anteroposteriorly, forming the articular surface for the calcaneum, being approximately equal depth in all three specimens. The transverse width of the articular facets is greater in *D. bennettianus* than *M. fuliginosus* which is in turn greater than *M. rufus* where the facets are longer anteroposteriorly and narrower transversely. The two facets for the calcaneum on the astragalus are more similar in shape in *M. rufus* and *M. fuliginosus* compared with *Dendrolagus*, where in the former two, the lateral facet is roughly circular, compared with the triangular form of the latter. Also in *Dendrolagus*, the medial facet is sub triangular compared with the transversely wide rectangular form of the medial facet for the calcaneum in *M. rufus* and *M. fuliginosus*. A small area of the lateroplantar portion of the head of the astragalus also articulates with a dorsomedial portion of the calcaneum.

Medially, the articulation for the medial malleolus varies slightly between the three specimens. In *Dendrolagus* there is an ovoid pit on the medial malleolus compared with a more circular pit in *M. fuliginosus* and *M. rufus*. The ridge on the medial aspect for the posterior tibiotalar ligament is longer in *M. rufus* than *M. fuliginosus* because of the elongated portion of the medial trochlear ridge. The site for the attachment of the posterior tibiotalar ligament in *Dendrolagus* is more angled, giving a greater area of attachment for the ligament dorsally compared with the nearly flat ridges of *M. fuliginosus* and *M. rufus*. The area for attachment of the anterior tibiotalar ligament is smallest in *Dendrolagus*, but is borne in a deep groove which lies medially and plantarly compared with *M. rufus* and *M. fuliginosus* where the site for attachment is predominantly on the medial surface, and also dorsally as illustrated by a deep pit in *M. rufus*.

Ventrally in medial aspect, the astragalus is curved concavely, most greatly in *Dendrolagus* and least curved in *M. rufus*. The other main distinction is with the articulation on the astragalus for the cuboid and navicular. In *Dendrolagus* the articular surface is curved gently convexly and runs nearly transversely, terminating medially compared with *M. rufus* and *M. fuliginosus* where this articular facet is directed dorsoplantarly. The largest articulation on the astragalus for the cuboid is in *M. rufus* where this articulation encroaches on the anterior or distal face of the head of the astragalus, so that the area on the astragalus for the navicular is reduced and narrow dorsally. This facet is also deflected more plantarly than in *Dendrolagus* and *M. fuliginosus*.

ii) The comparative anatomy of the calcaneum: The tuber calcanei of the calcaneum of *M. fuliginosus* and *M. rufus* is triangular in cross-section, being flattened and broad plantarly compared with *D. bennettianus* which is much shorter and broader and ovoid in cross-section, reminiscent of possums and koalas. The dorsal surface of the tubercalcanei is formed by two surfaces which converge dorsally into a longitudinal ridge which extends posteriorly. In *D. bennettianus* this ridge is very flat and broad, narrowing posteriorly. In *M. fuliginosus* this ridge is relatively narrow, but not as narrow as in *M. rufus*. There is considerable difference in the width of the sustentaculum tali of these three macropods. In *Dendrolagus* the sustentaculum tali is very broad transversely and pointed medially and shallow dorso-plantarly, compared with *M. fuliginosus* and *M. rufus* where the sustentaculum tali is very narrow, particularly so in *M. rufus*. Corresponding with the astragalus, the anteroposterior length of the sustentaculum tali is shorter in *D. bennettianus* than *M. fuliginosus* which is shorter than the very elongated form in *M. rufus*. The sustentaculum tali is deepest and most curved in *M. fuliginosus*. In *D. bennettianus* the plantar process of the sustentaculum tali extends further medially and nearly contacts the ground, compared with the slightly concave nature of the sustentaculum tali dorsoplantarly in the other two specimens. The sustentaculum tali also bears the tuberosity for the ligamentum cervicis tali on the dorsal surface and is larger in *M. rufus* than *M. fuliginosus* compared with *D. bennettianus*, where the deep groove for this ligament extends posteriorly on the medial surface. In *D. bennettianus* the sustentaculum tali bears a very shallow and broad groove for the tendon of flexor digitorum longus compared with the relatively deep groove of *M. fuliginosus* and *M. rufus*, and is more steeply inclined in the former. Laterally, the fibular condyle exhibits similar variation. The calcaneum has least area of contact for the fibula in *Dendrolagus*, and greatest in *M. rufus*. In *D. bennettianus* the lateral malleolar condyle is angled more obliquely than in the other macropods, as in the case with its medial malleolar condyle. Only *M. fuliginosus* and *M. rufus* bear a true condyle for the fibula, posterolaterally in the former and laterally in the latter. In *M. fuliginosus* and *M. rufus* there is an area excavated in the body of the calcaneum underneath the lateral projection which is not present in *D. bennettianus*. Dorsally the lateral border of the most distal portion of the calcaneum is directed medially in *M. fuliginosus* and *M. rufus* compared with *D. bennettianus*, where this section continues in the axial longitudinal plane of the foot.

There are two facets on the calcaneum for the astragalus. The lateral facet is nar-

rowest in *M. rufus*, almost circular, slightly wider in *M. fuliginosus*, and much broader transversely in *D. bennettianus* which narrows medially. This convex facet is separated from the concave medial facet in *M. fuliginosus* by a small longitudinal ridge, compared with *D. bennettianus* and *M. rufus* where it is nearly continuous between the two facets. In *M. rufus* and *D. bennettianus* the ridge of the medial facet is higher than the lateral facet. This ridge, which is curved in *M. fuliginosus* and *M. rufus*, is straight and runs transversely in *D. bennettianus*.

The fossa for the anterior proximal process of the astragalus which is a small circular pit in *M. fuliginosus*, is more ovoid anteroposteriorly in *M. rufus* and divided by a small ridge, and is not discernible in *D. bennettianus* as this portion of the calcaneum is flat and converges with the lateral border. The corresponding fossa in *D. bennettianus* is on the anterior face of the lateral facet for the astragalus. In *M. rufus* and *M. fuliginosus* there is a small triangular facet on the dorsoanterior medial portion of the calcaneum for articulation with the lateral border of the neck of the astragalus.

Distally, the dorsomedial facet on the calcaneum for the cuboid is transversely broad and rectangular in *M. fuliginosus*, equally broad and deep in *M. rufus* and triangular in *D. bennettianus*. This facet is convex dorsoplantarly, only slightly in *D. bennettianus*, moderately convex in *M. fuliginosus*, and strongly convex in *M. rufus*. The dorsolateral facet on the calcaneum for the cuboid in *M. fuliginosus* and *M. rufus* is narrower transversely and elongated dorsoplantarly. However in *D. bennettianus* this facet is transversely broad, and triangular in shape, narrowing laterally. This facet is convex dorsoplantarly and concave transversely only slightly in *D. bennettianus*, moderately in *M. fuliginosus* and strongly in *M. rufus*. There is a step between the dorsolateral and dorsomedial facets on the calcaneum for the cuboid which is subtle in *D. bennettianus* and lies oblique to the axis of the foot, slightly more acute in *M. fuliginosus* and in line with the axis of the foot in *M. rufus*. The dorsolateral facet merges into the ventromedian facet for the cuboid on the calcaneum, which is circular and slightly concave in *M. rufus*, circular and slightly convex in *M. fuliginosus* and barely distinguishable in the flattened surface of *D. bennettianus*. These three aforementioned facets in the three specimens are separated differently from contact with the ground by a sulcus. The plantar portions of the dorsomedial and ventromedian facets are in contact with the ground in *D. bennettianus* and *M. fuliginosus*, compared with *M. rufus* where the facets are separated by a large, deep sulcus.

iii) Comparative anatomy of the cuboid: Dorsally, the cuboid is greater in length medially than laterally in all of the specimens. The medial border is concave slightly in *M. rufus* and moderately in both *M. fuliginosus* and *D. bennettianus*. The fossa for the dorsolateral facet of the calcaneum for the cuboid is visible in dorsal view. This fossa is obscured in *M. rufus*, partly visible in *M. fuliginosus* and entirely visible in *D. bennettianus*. The step between the dorsolateral and dorsomedial facets of the calcaneum for the cuboid is also apparent on the proximal surface of the cuboid, and when viewed dorsally this angle is in line with the long axis of the foot in *M. rufus*, slightly oblique in *M. fuliginosus* and very oblique in *D. bennettianus*. The proximal portion on the medial side in *M. rufus* is deflected posteromedially to articulate with the astragalus, compared with *D. bennettianus* and *M. fuliginosus* where there is only small surface for articulation for the astragalus on the medial side. Also in dorsal view, none of the distal articulating facets can be seen in *D. bennettianus*.

Medially, the cuboids of *M. rufus* and *M. fuliginosus* are vastly different from that of *D. bennettianus*, the latter which is rhomboidal in appearance, while in the former pair they are rectangular, deep and anteroposteriorly compressed. The cuboid as in the calcaneum is greatly compressed dorsoplantarly. The fossa for the dorsomedial facet of the calcaneum can also be seen in cross-section, and it is greatly concave in *M. rufus*, slightly less concave in *M. fuliginosus* and only gently concave in *D. bennettianus*. Also prominent medially in *D. bennettianus* is a deep sulcus bearing the large cubonavicular

and mesocuneiform ligament. Medially in *D. bennettianus* the medial plantar process forms part of the plantar surface of the foot, being different from *M. fuliginosus* and *M. rufus* where the medial plantar crest is raised off the plantar surface to make room for the large tendon of flexor digitorum longus.

Anteriorly in medial aspect in *D.bennettianus* the cuboid is expanded dorsally where it is concave, and convex plantarly. In contrast, in *M. fuliginosus* and *M. rufus* the anterior profile of the cuboid is concave dorsally, convex in the median section, then concave again plantarly. Laterally, the cuboid is longest anteroposteriorly and shallowest dorsoplantarly in *D. bennettianus*. The lateral plantar crest is expanded anteroposteriorly in *M. rufus* and *M.fuliginosus*, compared to the very short lateral plantar crest of *D. bennettianus*. All three specimens have a deep tuberous sulcus for the insertion of the tendon of the peroneus longus.

Ventrally the most prominent feature of *M. fuliginosus* and *M. rufus* is their large ovoid lateral plantar process, separated from a smaller and shorter medial plantar process by a sulcus running longitudinally, the path of the ligament attaching the medial side of the cuboid to the base of the fourth and fifth metatarsals. In *D. bennettianus* the two plantar processes, which are of equal sizes, both make contact with the ground and are separated by an oblique sulcus running posterolateral to anteromedial region of the cuboid.

Distally, the cuboid bears three facets; the largest articulating with the fourth metatarsal, a smaller circular facet in *M. fuliginosus* and *M. rufus* or small triangular facet in *D. bennettianus* articulating with the plantar crest of the fourth metatarsal, which is a small rectangular facet in *M. rufus* and *M. fuliginosus* and a semicircular facet in *D. bennettianus*. The facet for the plantar crest of the fourth metatarsal, lying ventromedially is approximately the same size in all specimens, but is barely distinguishable in *D. bennettianus*, and is separated from the larger articular facet for the fourth metatarsal by a thin tuberous section. In *M. rufus* however these facets are separated by a small deep sulcus which channels the medial section of the ligament joining the cuboid to the fourth metatarsal. The size of the facet on the ventrolateral portion of the cuboid is largest in *D. bennettianus* and smallest in *M. rufus* compared with *M. fuliginosus*.

The Calcanea of extinct and extant Macropods

Statistical analysis

The results of the cluster analysis can be seen in Fig. 4. This figure is a diagrammatic representation of the output from the SPSS clustering algorithm. This analysis included both the fossil specimens and known extant specimens. If any one of the variables was missing from the measurements of one of the specimens, the respective specimen was excluded from the analysis (approximately 15% of the total sample). As a consequence, it was necessary to include the specimens not used in the analysis after the remainder of the calcanea were sorted out, using these as a guide.

Group "1" contains 14 specimens which are all definitely sthenurine, and most probably *Sthenurus brownei* (Merrilees and Porter 1979). There are two distinct size ranges in this group, and if one species is represented, this may be explained as sexual dimorphism. (see Fig. 6)

Group "2" contains 12 specimens and is also definitely sthenurine, most probably *Sthenurus occidentalis* (Merrilees and Porter 1979). This group contains four very large specimens, two of which still have their astragalus articulated. There are four medium sized calcanea and four smaller specimens, suggesting that this group may contain at least a second species, smaller than *S. brownei* and *S. occidentalis* (see Fig.7).

Group "3" contains 14 macropodine specimens. From examination and comparison with extant specimens, this group contains a majority of specimens attributable to *Macropus fuliginosus*, but also interestingly three specimens which can be identified as
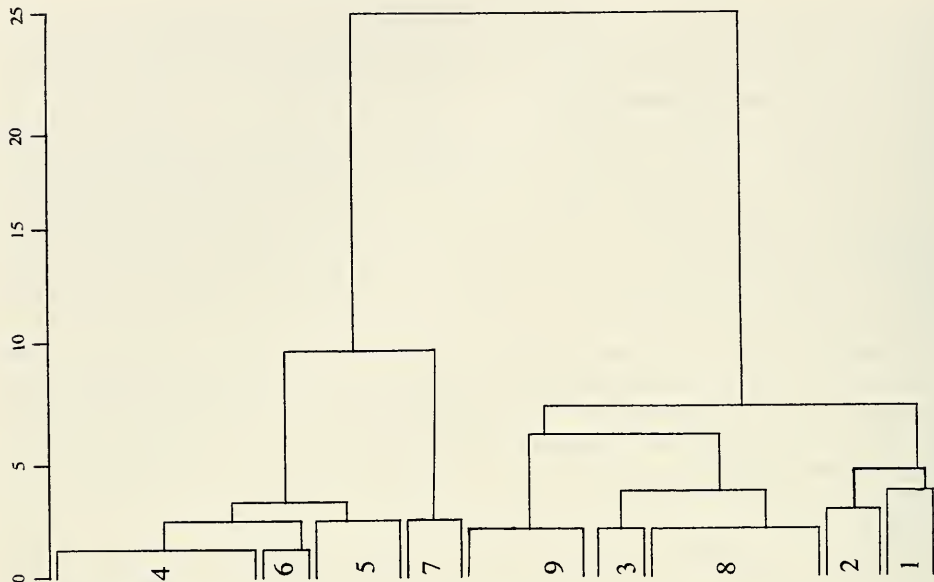
Figure 4. Shows the diagramatically simplified results of the cluster analysis performed on the fossilised cal-canea. Left-hand terminations represent the groups separated in the cluster analysis. This diagram gives a repre-sentative view of the similarity (indicated by the arbitrary scale of 0–25 on the y- axis) in structure of the groups clustered out in the analysis

Macropus rufus, an exclusively plains and desert-dwelling kangaroo. Using the measure-ments taken, the clustering algorithm assigned *M. fuliginosus* and *M. robustus* to this group. Due to the large size of the specimens, this group most likely contains the fos-silised calcanea of *M. fuliginosus* rather than the smaller *M. robustus*.

Group "4" is the largest macropodine group with 57 specimens. Of the extant material, *Macropus parryi*, *Macropus rufogriseus*, and *Wallabia bicolor* were assigned to this group through the cluster analysis. *M. rufogriseus* is one of the best represented macropodine species identified from cranial elements. There are three distinct size ranges in this group, the largest of which most probably represents *M. rufogriseus*.

Group "5" is a large group containing 29 macropodid specimens. *Macropus dor-salis* is the only extant species associated with this group through the cluster analysis. Despite the observation that all of the specimens are roughly equal in size, there are defi-nitely two distinct morphs in this group, varying in only a few characters which were not measured in the analysis. Therefore they did not sort or cluster separately.

Group "6" contains six macropodid specimens. Although similar in size to a female *Macropus fuliginosus*, no modern macropodid sharing the distinctive features of these specimens were found. Their form however is somewhat similar to one of the two morphologically different subgroups of group "5". Many specimens of this group were not included in the analysis because of the poor state of preservation common to the group. Many of the specimens were large yet slender, with many of the processes being broken or abraded.

Group "7" contains three macropodine specimens. Many of the known extant species had been clustered in this group; *Macropus parma*, *Macropus irma*, *Dorcopsus sp*, *Petrogale lateralis*, *Setonix brachyurus*, and *Macropus eugenii*. On comparison with extant material, only the latter was found to be represented in the fossil collection . It is interesting to note that so many extant macropodid species are found clustered together

in one group. This indicates that the genera represented are similar, and that the cluster analysis was not able to discriminate to the genus level in this cluster.

Group "8" contains 25 macropodid specimens. The majority of this group is probably attributable to *Macropus titan* or *Macropus giganteus*, and also possibly *Macropus robustus*. The cluster analysis assigned *Macropus fuliginosus* to this group. However, this is a recent lineage, and any such material pre or during the Pleistocene is often referred to as belonging to *Macropus giganteus*. There do seem to be two separate morphs within this group exhibiting very little size variation.

Group "9" is the largest sthenurine group with 34 specimens. It appears that this group could possibly be divided further into three separate morphs. Based on a comparison of the relative abundance of sthenurine cranial elements from the Victoria fossil cave deposit, the larger part of this group is probably attributable to *Sthenurus gilli*. This is supported by the observation that *Sthenurus gilli* is the smallest species from Victoria fossil cave deposit, which corresponds with the small size of the specimens. One morph may be attributed to *Sthenurus andersoni* (see Fig. 8).

It is now important to understand which factors are causing the main variation of the morphology of the characters measured. This is achieved through examination of the principal components analysis.

TABLE 5

The results of the principle components analysis and the first three factors (as defined in text) which account for the majority of the variation.

Factor	Eigenvalue	Percent of Variation	Cumulative percentage
1	8.926	81.8	81.8
2	0.891	8.1	89.2
3	0.362	3.3	92.5

Usually with a principal components analysis, a great deal of the variation for the entire data set can be explained by only two or three factors. Looking at Table 5 we can see that in this group of calcanea, 92.5% of the variation can be explained by the first three factors, shown in the cumulative percentage column. The majority of the variation is undoubtedly in the first factor, which is usually, and certainly in this case, attributed as size. Hence 81.8% of the variation is accounted for by size.

It can be seen from Fig. 4 that the sthenurine groups cluster separately from the larger macropodid group. This plot indicates that there were no small sized species among the sthenurines as seen in groups "4" and "7" of the macropodids. Only principle components with an eigenvalue greater than '1' are regarded as being statistically significant and hence through principal components analysis, size is the only statistically significant factor.

Comparative morphology of the sthenurine calcanea

As many of the groups sorted out can be assigned to a number of extant taxa, in which functional and morphological characters are well understood (Owen 1875, Parsons 1896, Windle and Parsons 1897, Craven 1971, Hopwood and Butterfield 1990), I will concentrate on the sthenurine groups. Where more than one species has clustered into a single group of the extant macropods, it was possible to discern between the different species through a visual examination. Within each group there are at least two or more morphs. These morphs most probably relate to separate species or perhaps separate sexu-

Figure 5. The right calcaneum of *Macropus fuliginosus* in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **DIV**- longitudinal division of the medial and lateral facets on the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS**- Plantar process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS**- Transverse plantar sulcus.

al morphs of the same species. Marked sexual dimorphism is exhibited in modern kangaroos by way of size (Poole et.al 1984). As the clustering algorithm used removes the factor of size, it is expected that sexually dimorphic species will group into the same cluster. Within group (1) there are at least two morphs; three morphs in group (2); and three morphs in group (9) (see Figs 6–8). The figures follow after the text.

The tuber calcanei of *Macropus fuliginosus* is of sub triangular form. Of the sthenurines, morph (iii) of group (9) possesses an ovoid cross sectional shape of the tuber calcanei (see Figs 5 and 8). The remainder of the sthenurines possess a generally much broader tuber calcanei which is sub triangular in morphs (i) and (ii) of group (1), morph (i) of group (2), and morph (ii) of group (9), compared with the square cross sectional shape of morphs (ii) and (iii) of group (2), and morph (i) of group (9) (see Figs 6–8). All of the specimens narrow dorsally to some extent and are flattened plantarly. The tuber calcanei is flared greatly posteriorly in the sthenurines compared with *M. fuliginosus*. The medial and lateral surfaces of the tuber calcanei apex in a longitudinal ridge which is narrow in morphs (ii) and (iii) of group (9) compared with *M. fuliginosus* (see Figs 5 and 8). Of the other sthenurines, this longitudinal ridge is moderately narrow in group (1),

Figure 6. The right calcaneum of a representative of group "1" in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS**- Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS**- Transverse plantar sulcus.

broad in all morphs of group (2), but most broad and nearly continuous with the medial and lateral surfaces in morph (i) of group (9). The tuber calcanei is also deepest in morph (iii) of group (9) relative to its width (see Fig. 8). The tuber calcanei is also shorter in the sthenurines than *M. fuliginosus* with the exception of all in group (1) and morph (iii) of group (9) (see Figs 5, 6 and 8). The sustentaculum tali is relatively narrow transversely in the sthenurines compared with *M. fuliginosus*.

A major difference in the sustentaculum tali in dorsal aspect is that in all of the sthenurines there is a posterior deflection of the plantar portion of the sustentaculum tali compared with *M. fuliginosus*, where the plantar portion of the sustentaculum tali is less angled and deflected medially (see Fig. 5). The sustentaculum tali is very much deeper

Figure 7. The right calcaneum of a representative of group "2" in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS**- Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS**- Transverse plantar sulcus.

dorsoplantarly in all of the sthenurine species than in the two macropodine specimens (see Figs 5–8). Another feature common to all of the sthenurines is that the plantar surface of the sustentaculum tali points directly plantarly compared with anteroplantarly in group (6) and *M. fuliginosus* (see Figs 5–8). The plantar process of the sustentaculum tali makes up part of the plantar surface in morphs (i) and (ii) of group (2) as well as morphs (i) and (ii) of group (9) (see Figs 7 and 8). In the remainder of the sthenurine groups the plantar process of the sustentaculum tali is separated from the plantar process by a dorso-plantarly deep groove for the tendon of the flexor digitorum longus. This separation from the plantar surface is most extreme in morph (iii) of group (9). Another main distinction between the sthenurines and the macropodines can be seen in the medial profile of the sustentaculum tali, where in the sthenurines, because of the plantarly deflected plantar process, a right angle or 90° profile is produced. This is in contrast to *M. fuliginosus*,
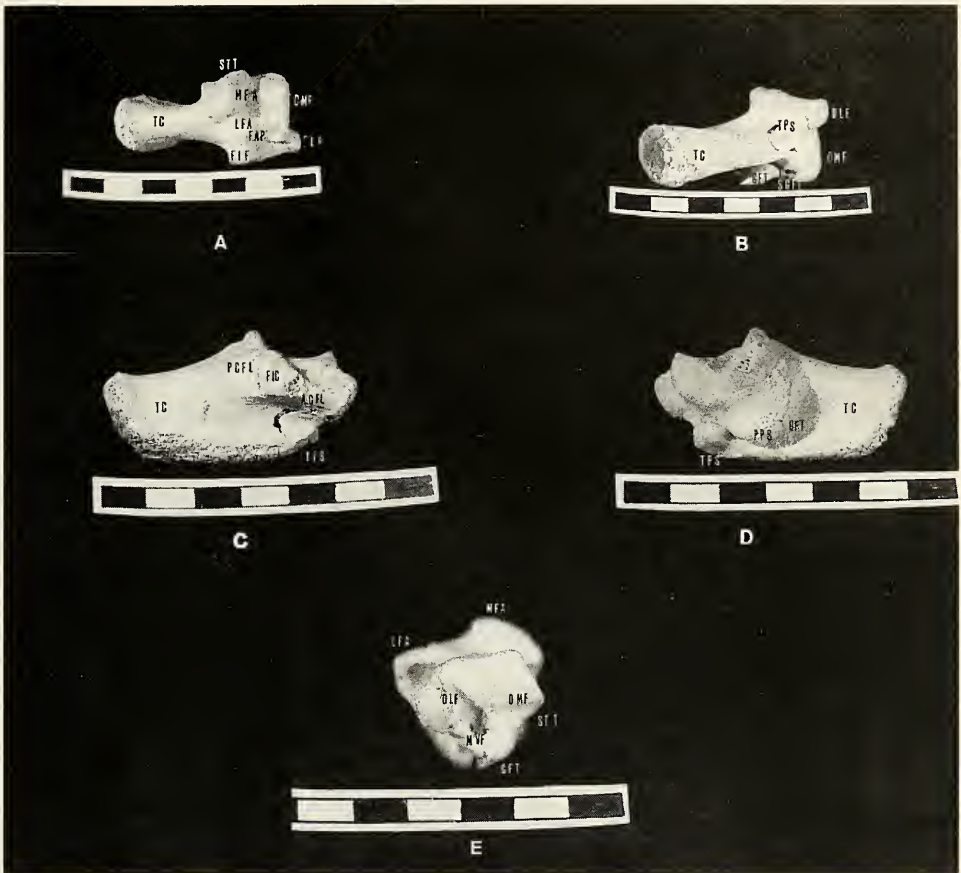
Figure 8. The right calcaneum of a representative of group "9" in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS**- Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS**- Transverse plantar sulcus.

where the border is rounded posteriorly and not so steeply inclined, as also noted by Murray (1995) (see Figs 5–8).

Laterally the fibular condyle is not as wide in sthenurines as it is in *M. fuliginosus*. Dorsally, the fibular condyle is substantially variable between the different morphs of the different groups, but generally the origin of the condyle being more abrupt in the sthenurines than macropodines. Laterally the fibular condyle bears two scars; one posteriorly for the posterior calcaneofibular ligament and one anteriorly for the anterior calcaneofibular ligament. In morph (i) of group (1) the scar for this ligament encroaches dorsally on the condyle, also providing an area for the posterior talofibular ligament which intervenes in between the fibula and its condyle (Fig. 6). The angle of the scar for the posterior calcaneofibular ligament is also slightly vertically inclined, but not as much as in *M. fuliginosus* (Fig. 5). The posterior border of the fibular condyle is also more abrupt

in morph (i) than morph (ii) of group (1), compared with *M. fuliginosus* where the fibular condyle is curved convexly plantarly and then recurved, demarcating the scar for the attachment of the anterior calcaneofibular ligament. The fibular condyle is also generally deeper in the sthenurines than in *M. fuliginosus*. In all of the sthenurines there is also a greater area for insertion of the lateral calcaneocuboid ligament.

Dorsally, there are two facets on the calcaneum for articulation with the astragalus. The origin of the lateral facet for the calcaneum on the dorsal surface is markedly variable in the different specimens. In morph (i) of group (1), the lateral facet for the astragalus originates from and is continuous with the dorsolateral surface as in morph (iii) of group (9), compared with *M. fuliginosus*, where although the lateral facet for the astragalus originates from the dorsolateral surface of the tuber calcanei, it is interrupted by the higher convex form of the facet. In the remainder of the sthenurines the origin of the lateral facet for the astragalus is dorsally from the tuber calcanei, and is interrupted by its convex form in morph (ii) of group (1), morphs (i) and (ii) of group (2), and morph (i) of group (9), compared with morph (i) of group (1), morph (iii) of group (2), and morph (ii) of group (9) where the origin of the facet is continuous with the dorsal surface of the tuber calcanei. Immediately anterior to the lateral facet for the astragalus is the fossa for the proximal ventrolateral process of the astragalus, which is generally much deeper in the sthenurines. This fossa is also expanded anteroposteriorly in morph (ii) of group (1), and morph (i) of group (2), rather than being transversely broad in the other sthenurines, compared with the shallow circular pit in *M. fuliginosus* (see Fig. 5). In all of the sthenurines, the lateral facet for the astragalus sits lower than the medial facet. The medial facet for the astragalus is similarly variable between the sthenurines and macropodines, as well as within the sthenurines. Generally the medial facet for the astragalus is steeper in the sthenurines than in *M. fuliginosus*, which is shallowly concave on its anterior face and inclined posterodorsally (see Figs 5–8). The lateral and medial facets for the astragalus are separated by a transversely convex ridge which is particularly high and narrow in morph (ii) of group (1), morph (i) of group (2), and morph (i) of group (9), and slightly more shallow but still convex in morph (i) of group (1), morphs (ii) and (iii) of group (2), and morphs (ii) and (iii) of group (9). This feature may allow a slight degree of pronation. However in *M. fuliginosus* the lateral facet sits as high as the medial facet and is separated from the latter by a small longitudinal ridge, restricting pronation and supination. Directly behind the medial ridge which articulates with the astragalus, there is a scar for the posterior talocalcaneal ligament, the main posterior ligament binding the astragalus to the calcaneum. This scar in sthenurines suggests that the ligament, which is deflected dorsally and posterolaterally in *M. fuliginosus*, is deflected only dorsally, restricting any motion of the astragalus rolling forward. The pit for this ligament is greatest in morph (ii) of group (1) and morph (i) of group (9) (see Figs 5–8).

On the posterodorsomedial region of the sustentaculum tali is a large scar for the posteromedial talocalcaneal ligament in the sthenurine groups, perhaps with the exception of morphs (ii) and (iii) of group (9) where the scar is smaller compared with *M. fuliginosus*. The sustentaculum tali bears much of the weight of the astragalus in the majority of sthenurine morphs, with the exception of (ii) and (iii) of group (9). It is elongated anteroposteriorly at its dorsal margin compared with *M. fuliginosus* where it narrows dorsally.

In dorsal aspect it is also possible to see the varying morphology of the dorsolateral facet on the calcaneum for the cuboid. In all of the sthenurine groups, the dorsolateral facet is more narrow transversely, generally shorter anteroposteriorly, but more importantly the medial side of this portion is deflected laterally, i.e. the calcaneocuboid step is not as steep as in *M. fuliginosus* (see Figs 5–8). The dorsolateral facet is shortest in morph (iii) of group(2) and morph (ii) of group (9), which exhibit the shallowest step. This process is steepest and most elongate in morphs (i) and (iii) of group (9) (Fig. 8). The remainder of the sthenurines are somewhat intermediate in this character. The shallower the angle of the calcaneocuboid step on the calcaneum, the greater the ability for

supination of the foot at the calcaneocuboid joint.

Ventrally, the plantar surface of the calcaneum is very greatly elongated in *M. fuliginosus*. This is due in great part to the width and position of the transverse plantar sulcus. This is narrowest and situated anterior most among the sthenurines in morphs (i) and (ii) of group(1), and morph (i) of group (9), and hence the greatest plantar surface length. It is also broadest anteriorly in the formerly mentioned morphs and *M. fuliginosus* compared with morphs (i) (ii), and (iii) of group (2) and morphs (ii) and (iii) of group (9). Here the plantar surface is narrow anteriorly and emanates from the lateral side. It is expanded posteriorly, particularly in morphs (i) and (iii) of group (2) and morph (ii) of group (9) and results in the plantar surface being nearly triangular in form (see Figs 7 and 8). In *M. fuliginosus* the plantar surface is nearly uniform in transverse breadth along its length, expanding only slightly posteriorly. The plantar surface is most narrow in morph (iii) of group (9). A large component of variation can also be seen plantarly in the comparative widths of the groove for the tendon of the flexor digitorum longus which is greatest in morph (ii) of group (1), morph (i) of group(2), and morph (i) of group (9) (see Figs 6, 7 and 8). Correspondingly the groove in the aforementioned specimens is only shallowly concave transversely compared with *M. fuliginosus*. Conversely it is deeply excavated and concave in morphs (ii) and (iii) of group (2), morphs (ii) and (iii) of group (9), and to a lesser extent morph (i) of group(1). In all of the sthenurines there is a demarcation at the base of the sustentaculum tali in the form of a narrow longitudinal sulcus which is not present in *M. fuliginosus*.

Distally, there are three facets on the calcaneum which articulate with the cuboid. In general, the dorsomedial and dorsolateral facets on the calcaneum are more narrow transversely, although still quite broad in morph (i) of group(1) and morphs (ii) and (iii) of group(2), compared with *M. fuliginosus* (see Figs 5–8). The medial border of the dorsomedial facet on the calcaneum for the cuboid is steeper in the sthenurine groups and nearly vertical in morph (iii) of group (2) compared with *M. fuliginosus*, which is deflected dorsomedially. The dorsolateral facet on the calcaneum for the cuboid is also more elongated dorsoplantarly in the sthenurine groups than *M. fuliginosus*. Also characteristic of the sthenurines this facet sits lower, or starts more plantarly in distal aspect to the larger dorsomedial facet, compared with *M. fuliginosus* where the dorsolateral facet for the cuboid is equal in height to the dorsomedial facet for the cuboid (see Figs 5–8). The dorsolateral facet is also deflected dorsomedially in morph (ii) of group (1), morph (i) and (iii) of group (2) and morph (i) of group (9). Where the dorsolateral facet for the cuboid is expanded in the sthenurine groups, as in morph (ii) of group(1), morph (i) of group (2) and morph (i) of group (9), it is done so more plantarly, approximately half the way down the distal surface. The lateral border of the lateral facet for the cuboid is curved convexly dorsoplantarly in the dorsal region then recurves concavely more plantarly, most strongly convex dorsally in group (6), morph (ii) of group (1), morph (i) of group (2), and morph (i) of group (9), and most concave plantarly in morphs (i) and (iii) of group (2), and morphs (ii) and (iii) of group (9) (see Figs 5–8). The dorsolateral facet narrows plantarly and merges into the ventromedian facet which is generally larger in the sthenurine groups than *M. fuliginosus*. In morphs (i) and (ii) of group (1), morphs (i) and (ii) of group (2), morph (i) of group (9), the plantar portion of this facet contributes to the plantar surface of the pes. In morphs (i) and (ii) of group (2) and morph (i) of group (9), the apex of the ventromedian facet is situated directly underneath the dorsomedial facet compared with the more medial placement of the facet underneath the step separating the dorsomedial and dorsolateral facets in *M. fuliginosus*, morph (iii) of group(2), and morphs (ii) and (iii) of group (9). It is common to all of the aforementioned morphs that the ventromedian facet plays no direct weight bearing role. Common to all of the sthenurine groups is the curved form of the ventromedian facet, whose dorsal and plantar borders are curved transversely such that the facet is "u" shaped in morphology compared with *M. fuliginosus*, which possesses a small ovoid facet. Also common to the sthenurine groups is the merging of the

ventromedian facet on to the dorsomedial facet for the cuboid, making the three facets continuous, and forming a fossa in the centre of the three facets, compared with *M. fuliginosus* where the two facets are separated by a deep groove (see Figs 5–8).

DISCUSSION

The plesiomorphic characters of the marsupial pes

In constructing the cladistic relations of this group, it was revealed that there were no phylogenetic reversals in the cladogram. The pes of the outgroup expressed fourteen of the seventeen characters that were considered to be symplesiomorphic. This indicated that the morphology of the pes is highly conservative. There were only three characters where the polarity could not be determined. These were: 1 - (Character 10) The tuber calcanei, which was phylogenetically uninformative due to its diverse morphology. Murray (1995) similarly found this character to be uninformative in his study of the phylogenetic relationships of the late Miocene kangaroo, *Hadronomas*. 2 - (Character 5) The possession of a trochlear notch along with the (plesiomorphic) long astragalar head and neck in the wombat can be attributed to parallelism of evolution. Similarly the convergence in form of the sustentaculum tali of the koala and *Hypsiprymnodon* is unlikely to be the result of similar function in these species. The expression of this character state in the koala may be attributed to the retention of an ancestral character state. 3 - (Character 11) Based on a single feature, the Potoroidae would appear to be derived from the Phascolarctidae, contradictory to current phylogenetic placement. The contradictory nature of the cladogram can be explained by the use of a limited character set, i.e. the groupings of the outgroup marsupials are being determined on only one or two characters which are seen to be divergent from the generalised marsupial pes. This is most probably biased through the choice of characters which seemed to be most divergent in the macropodid species. A larger set of characters would have to be used for a more comprehensive study, particularly for the plesiomorphic states.

There were six shared derived features which unite *Hypsiprymnodon* (the most Plesiomorphic of the living kangaroos) with *M. fuliginosus*. This is consistent with the current placement of this family and its contained species, as intermediate in structure between the phalangerids (possums) and the macropodids (kangaroos). Disregarding the uninformative characters (5,10 and 11), there were no reversals of characters between the ancestral marsupial grade and that of *M. fuliginosus*.

The derived features of the macropodine pes are considered to be important, as they define its specific structure in relation to the generalised marsupial pes. Those features which are characteristic of the macropodines are likely to be related to locomotion and habitat preference. A more complete analysis of the features of the generalised macropodine form was attained through an examination of *Macropus fuliginosus* which is considered to be derived relative to *Hypsiprymnodon*. It is necessary to understand the functional nature of unique derived features of the macropodine pes.

Anatomy of the Hindlimb and Pes of Macropus fuliginosus

The results of this work support earlier findings (Craven 1971, Parsons 1896 Adnams-Hodges 1988, Hopwood and Butterfield 1990) that the main contribution to the muscle mass in the macropodines is in the flexor and extensor muscles of the hindlimb. This reflects the specialised form of locomotion. The actions of the separate muscles of the crus on the pes have been further described. The insertion points of the tendons and ligaments produce scars or rugosities on the surface of the bones. This knowledge has been used to identify homologous features on the bones of the extinct forms.

The functional anatomy of the western grey kangaroo, *Macropus fuliginosus* was used in this study as a general model against which to compare other macropodid species.

Also studied was the anatomy of the binding ligaments of the pes, an area which seems to have been ignored in previous studies. The main muscles acting on the pes have lines of action predominantly in the sagittal plane. Ligaments of the pes also tend to restrict motion to the sagittal plane. Ligaments also restrict the elongated pes from being excessively dorsiflexed. These ligaments are the large posterior and anterior calcaneofibu-lar ligaments in lateral aspect, and the posterior tibiotalar ligament and tibiocalcaneal liga-ment in medial aspect. Their cruciate (crossed) form stabilises the ankle. Similar results were found by Lewis (1983), and by Parsons (1896) who highlighted the stabilising nature of the "X" formation in the rock wallaby, *Petrogale xanthopus*. Parsons (1896) also iden-tified two calcaneocuboid ligaments, a large plantar ligament, referred to as the '*outer lig-ament*' running from the rugose plantar surface of the calcaneum to the lateral tubercle of the cuboid, and on to the base of the fourth and fifth ligaments; '*the medial*', being small-er but still prominent, passing from the sustentaculum tali to the cuboid and the base of the second and third metatarsals. These results complement the findings of this research. I conclude that the function of these ligaments is to prevent over dorsiflexion of the pes, and allow for the possibility of elastic recoil, loaded when the animal lands.

The most complete description of the macropodine foot to date is by Owen (1875) in his description of the pes of *Macropus rufus*. The work of Owen (1877–1878) supports the current findings, in that the narrow form of the pes is related to its saltatory mode of locomotion. Lewis (1980, 1982) also notes the form of the astragalus (a functionally important bone of the ankle) as being remodelled into a trochlear shape, convergent in function with the placentals, supporting the current findings. Conclusions regarding the splint-like nature of the fibula in macropods and its role in restricting the motion about the ankle to the sagittal plane are supported by Barnett and Napier (1953). One peculiarity of this form in macropods is that while the trochlear ridges of the astragalus are parallel, they are slightly oblique to the long axis of the foot, resulting in internal rotation of the foot. This may be linked to the idea expressed by Barnett and Napier (1953), Parsons (1896), and Wells and Tedford (1995), of the possibility of a spring return of the fibula when loaded as the lateral condyle of the femur forces the head posteriorly during flexion of the knee. With the pes firmly placed on the ground, the tibia, fibula and remainder of the ani-mal passes over the fixed pes, and the angle of the trochlear crests will act to rotate the crus externally, such that the action of the femur on the fibula is magnified. Parsons (1896), Windle and Parsons (1897), and Hopwood and Butterfield (1990) also provide evidence on the general morphology of the macropodine pes which supports the current study. The transverse nature of the subtalar joint complex was identified supporting earlier findings of Owen (1877–1878), Lewis (1964, 1980, 1983), and Barnett (1970).

Modifications of the macropodine pes.

Despite being restricted by the specialised mode of locomotion and necessary structural modifications associated with it, the modern macropods have managed to occupy a number of diverse habitats; e.g. as *Macropus rufus*, a plains dwelling kangaroo, and *Dendrolagus bennettianus*, a kangaroo adapted for an arboreal lifestyle.

Modifications of the Macropodid Pes for Open Plains and Arboreal Habitats

The main difference of the pes of *Macropus rufus*, an open plains animal, from that of *Macropus fuliginosus*, is the gracile form of the entire pes. As *M. rufus* inhabits large areas of flat treeless rolling plains of calcareous clay soils it is often referred to as the "open plains kangaroo". *M. rufus* also has the highest recorded speeds among modern macropodines (Bennett 1987).

There are a number of features of the pes of *Dendrolagus bennettianus* which I con-

sider to be adaptations to an arboreal lifestyle. Despite the macropodines having evolved from the arboreal possums, there is little doubt that *Dendrolagus* is a macropodine and not simply an ancestral grade between the possums and the kangaroos. It has clearly secondarily modified a terrestrial hindlimb for an arboreal lifestyle. Those features considered to be derived in the macropodine pes are also expressed in *D. bennettianus*.

i) Modifications of the Astragalus: The main distinction between *Dendrolagus* and *Macropus fuliginosus* is the form of the transversely broad astragalus. This feature is in accordance with the general breadth of the entire pes of this genus. The broad pes is a functional requirement for the arboreal habitat, giving greater stability on narrow tree limbs. The parallel trochlear crests are oblique to the long axis of the foot. In this respect the form is convergent in function with the other arboreal species examined in this study, the possum and koala. The oblique nature of the articulation of the crus on the pes results in one of two actions. With the proximal portions of the hindlimb held close to the body, when climbing, the oblique trochlear ridges cause the foot to be internally rotated, conceivably aiding in climbing tree trunks. Similarly when the feet are closely placed next to each other, such as when sitting on a branch, the knees are externally rotated, lowering the body and centre of gravity, resulting in a more stable posture.

Conforming with the remainder of the pes, in *M. rufus* the astragalus is relatively narrow transversely, and elongated anteroposteriorly. It is probable that the great anteroposterior length of the astragalus and of the trochlear ridges have the effect of restricting motion of the pes to the sagittal plane. The parallel trochlear ridges are in line with the longitudinal axis of the foot, indicating that any movement of the pes is confined to the sagittal plane. Another feature of this articulation in *M. rufus* is the medial trochlear ridge, which is greater in height than the lateral trochlear ridge and associated with a well demarcated and steep medial malleolus. This feature seems to be related to maintaining the pes in the sagittal plane during locomotion. Another factor restricting motion at this joint is the line of action of the main medial ligaments. Medially, the insertion of the two crossed ligaments on the astragalus are defined by a long horizontal ridge. This arrangement limits external and internal rotation of the pes as well as pronation.

The trochlear groove for the tibia is deepest in *Dendrolagus*, which I believe is due to the necessity for greater mobility at the ankle, in particular in being able to pronate and supinate the foot. When viewed in distal aspect, the medial and lateral trochlear ridges are equal in height compared with *Macropus fuliginosus* where the medial trochlear ridge is higher. I believe this is also related to the ability to pronate and supinate the foot. Barnett and Napier (1952), Hicks (1953), Close (1956) and Sarrafian (1993) have examined the nature of the ankle articulations in human specimens. Their results support the findings of this work that flexion and extension of the foot also affects other motions, such as pronation, and supination. Barnett (1970) and Lewis (1980) note the transverse nature of the subtalar joint complex, and Barnett (1970) notes the diverse morphology of this feature among the modern macropodines, but makes no functional interpretations.

Ventrally the articular facets of the calcaneoastragalar articulation are transversely broad, and this is most likely related to the general breadth of the pes. In *Dendrolagus* the medial malleolar tibial articulation is ovoid, expanded anteroposteriorly, and is probably related to greater mobility of the tibia. In *Dendrolagus* the scar for the posterior tibiotalar ligament suggests that the action of this ligament would most likely allow for greater eversion and inversion of the foot. Similarly the area for attachment for the anterior tibiotalar ligament is much reduced, possibly allowing for greater supination when the foot is plantarflexed, although even the reduced ligament would constrain this range of motion. The navicular facet on the astragalus is transversely wide, corresponding with an enlarged fifth digit. Lewis (1980) notes the nature of an intra articular meniscus in possums, which is much reduced in macropodids. Lewis (1980) also suggests the meniscus provides greater mobility at the articulation between the fibula, tibia, and the astra-

galus. Examination of a dried ligament preparation from the South Australian Museum indicated that the meniscus is enlarged in *Dendrolagus* compared to other macropodines.

ii) Modifications of the Calcaneum: The general morphology of the calcaneum of *Dendrolagus* corresponds with the form of the rest of the pes, being broad and dorso-plantarly compressed. The tuber calcanei is ovoid, reminiscent of the form of the possum, and considering its similar habitat, may also be convergent in function. Similarly, the sustentaculum tali is extremely broad, tapering medially as in the koala and possum, also related to the breadth of the pes. The sustentaculum tali bears a groove for the tendon of the flexor digitorum longus, the function of which is to flex the digits. The morphology of this groove in *Dendrolagus* is such that the tendon would be relatively unconstrained, allowing the digits to be flexed in a greater range of positions. There is a reduced articulation of the fibula with the calcaneum in *Dendrolagus*, as noted by Barnett and Napier (1953). This would suggest greater mobility at the articulatio tarsocruralis (between the crus and the pes) as the constraining nature of the talofibular articulation is minimised. This is associated with only a slight lateral projection for the fibula articulation.

In *M. rufus* the tuber calcanei shows evidence of being adapted to a biomechanical function, associated with an open plains habitat, as it narrows dorsally. Ontogenetic changes of bone are related to the direction and type of forces placed on it (Hildebrand 1988). As the tuber calcanei narrows dorsally, to a shape which is essentially triangular, it is indicative of the unidirectional forces acting upon the calcaneum. The groove for the tendon of the flexor digitorum longus runs under the very narrow sustentaculum tali, suggesting that the digits are only flexed when the foot is in the sagittal plane of the body, i.e. only when there is a direct line of action for this tendon. Dorsally, the large area for insertion of the ligamentum cervicis tali is associated with the strong binding of the astragalus to the calcaneum. This further restricts motion at the subtalar joint.

Another feature of the calcaneum suggesting a restriction of motion to the sagittal plane, is the size of the articular facet for the fibula. The fibula and the associated ligaments ensure the crus is securely braced to the pes, and restricts any internal or external rotation of the foot about the tibia. There are also a number of features of the ankle of *M. rufus* that relate to restriction of lateral movement at the calcaneocuboid articulation. This is supported by the arrangement of the ligaments at this joint. The dorsolateral facet of the calcaneum for the cuboid is anteroposteriorly compressed, but more importantly the step between this and the dorsomedial facet is well defined. This feature constrains any pronatory or supinatory motions of the pes.

Ventrally, the plantar surface of the pes is particularly tuberous, providing a large surface area for insertion of the plantar calcaneocuboid ligament. Medially, the sustentaculum tali is also tuberous for the insertion of a large medial calcaneocuboid ligament. These findings concur with those of Parsons (1896). The areas for insertion of the ligaments binding the cuboid to the fourth and reduced fifth metatarsal are also correspondingly large.

Dorsally, of the two articulating facets for the astragalus, the medial possesses a ridge dorsally which is straight, runs transversely, and is deflected slightly anteriorly. The function of this is probably for greater flexion and extension of the pes at the subtalar ankle joint. Directly behind this ridge is a large scar for the posterior talocalcaneal ligament, suggesting that the astragalus is well bound to the calcaneum posteriorly, resisting excessive pronation of the pes. A further feature of the talocalcaneocentralis joint of *Dendrolagus* is the fossa for the anterior proximal process of the astragalus is not well developed, and hence motion at this articulation is not restricted.

In summary, the features of the subtalar joint complex of *Dendrolagus* allow for greater freedom of movement associated with an arboreal habitat. Distally the main features of the calcaneum that allow for increased motion at the distal joint are related to the shallow gradient of the normally steep facets for the cuboid as expressed in other macropodines. The basic form of the distal articular surface is shallowly convex, both

transversely and dorsoplantarly (cup shaped), and corresponds to what Sarrafian (1993) describes as a male ovid surface. The motions generated at a male and female ovid (or ball and socket) joint are those of flexion, extension, pronation, supination, internal rotation, and external rotation (Sarrafian 1993).

iii) Modifications of the Cuboid: The proximal articulating facet of the cuboid corresponds with the calcaneum as the female ovid surface. As with the calcaneum and astragalus, the cuboid is transversely broad and dorsoplantarly compressed. Distally, the separate articulating facets on the cuboid for the fourth and fifth metatarsals take the form of a single facet. In medial or lateral view, the cuboid is rhomboidal in appearance, extended anteriorly dorsally, the function of which would be to prevent excessive dorsoflexion of the foot, being restricted by the protruding dorsal portion. Ventrally, in *Dendrolagus*, the medial plantar crest of the cuboid is enlarged, and in contact with the substrate surface, providing greater stability for the pes.

In summary, the feature of the *Dendrolagus* pes provides greater stability in the width of the pes in addition to greater mobility of the ankle joints, both necessary for an arboreal habitus.

These results suggest the main adaptations for an open plains habitat are an elongated narrow pes with motion restricted to the sagittal plane. The comparison of these two forms (arboreal and terrestrial), clearly indicate a large degree of homoplasticity in the features deemed to be derived within the macropodines. This has allowed the macropodines to radiate into a number of different habitats.

The Cluster Analysis

One aim of this study was to sort the fossilised calcanea from the Victoria Fossil Cave, Naracoorte. From an examination of both the cluster analysis and principal components analysis it can be seen that sthenurines separate from the macropodines and form three distinct groups. A closer examination of the group revealed a number of features of the calcaneum which were species specific. In a similar fashion, it is possible that the sthenurine groups may include more than one species.

The cluster analysis was an invaluable tool in determining primary structural differences in the large number specimens examined. It was not until after a discrete functional and structural analysis had been carried out that a number of "species specific" characters could be recognised.

Functional Anatomy of the Sthenurine Pes

Very few studies (Stirton 1963, Tedford 1966, 1967; Adnams-Hodges 1988; Murray 1991, 1995; Wells and Tedford 1995) have attempted to determine the functional nature of the postcranial elements of the sthenurines. Wells and Tedford (1995) examined the postcranial remains of three species of extinct sthenurines and suggested that as there are no modern descendants it was difficult to determine the locomotory habits of these animals for lack of a reliable functional analogue. These authors were however able to relate a number of features relating to the locomotor ability of the sthenurines. Wells and Tedford (1995) suggest that the sthenurine's mode of locomotion was of limited manoeuvrability, and further suggest that adaptations of the hindlimb and pes are related to supporting the weight of the animal, both during locomotion and stand-up browsing.

Just as the modern macropodine forms have diversified into a wide range of habitats, with accompanying differences in foot structure, so it is expected that differences in morphology of the calcaneum of the extinct forms may also be related to habitat.

The morphology of the tuber calcanei is much varied in the sthenurine morphospecies. Despite being generally more robust than *Macropus*, the four morphospecies share a subtriangular form; three of which have a square cross-sectional shape, and the fourth is

transversely narrow. The three 'species' where the tuber calcanei is square in cross-section suggest that forces acting on this process of the calcaneum are both in the sagittal and transverse planes. The transversely narrow tuber calcanei is indicative of forces being directed largely in the sagittal plane only. With the exception of four species, the tuber calcanei of the sthenurines is relatively anteroposteriorly compressed. This would suggest that the sthenurines were not as well adapted for fast locomotion as many of the extant macropodines. Their form is divergent from the form of the highly specialised red kangaroo, *Macropus rufus*. As noted by Tedford (1966, 1967), Adnams-Hodges (1988), Murray (1995), and Wells and Tedford (1995), the sustentaculum tali is generally narrower in the sthenurines than the macropodines, with the exception of two morphospecies where the sustentaculum tali is particularly broad posteriorly. This seems to be convergent in function with the possums and koalas, in being an adaptation allowing the digits to be plantar flexed while the foot is internally rotated. This is supported in other features of the sustentaculum tali. In medial aspect, the profile of the sustentaculum tali is dorsoplantarly deep and right-angled, providing two possible functions. While the main extensor muscles, the gastrocnemius and flexor digitorum brevis provide the majority of the power to extend the pes during standing, the flexor digitorum longus may augment this action. As the animal starts to stand, the distal digits are firmly planted on the ground, and the action of the tendon of the flexor digitorum longus running underneath the pes would be to elevate the pes at the point of the sustentaculum tali. The right angled form of the sustentaculum tali would also impede the tendon from dislodging medially. This is supported by another feature of the sustentaculum tali in that it is pointed plantarly, further constraining the tendon with the foot extended, and also possibly providing support medially, as it contributes to the plantar surface of the pes in all but one morphospecies.

Also related to the action of the flexor digitorum longus tendon across the sustentaculum tali is the presence of a small longitudinal groove lateral to the path of the tendon, separating the sustentaculum from the body of the calcaneum plantarly, also reported by Wells and Tedford (1995). Deep within this groove is a small foramen, which suggests that this adaptation is for protection of the blood and nervous innervation of the calcaneum. Another feature of the calcaneum related to raising the body is the degree to which the tuber calcanei is flared posteriorly. On comparison of sthenurine and macropodine specimens of equal size, this feature indicates large areas for insertion of the tendons of the gastrocnemius and flexor digitorum brevis, suggesting that the action of these tendons in extending the pes is particularly important in the sthenurines, supporting earlier findings (Adnams-Hodges 1988, Murray 1989, 1995, and Wells and Tedford 1995).

The fibular condyle is reduced in the sthenurines and relatively flat compared with *M. fuliginosus*, indicating less fibular contact with the calcaneum. On many of the sthenurine calcanea, the fibular condyle is depressed, sitting lower on the lateral face. This may indicate that the foot is able to be pronated to a greater degree, supporting the suggestion of Murray (1995) that the majority of the weight is transferred to the medial side in the sthenurines. This is further supported by a number of features of the calcaneum. If the sthenurines were to distribute the majority of their weight medially, with their foot pronated, we would expect to see a number of mechanisms preventing the astragalus from being displaced from the calcaneum. One of the most notable pieces of evidence for this is the large scar for the calcaneoastragalar ligament, which is similarly large in the arboreal forms, possum, koala, and tree kangaroo. This was also noted by Stirton (1963), and Murray (1995). This ligament restricts anteromedial movement of the astragalus about the calcaneum. The medial articulation for the astragalus is greatly accentuated and bears a deep scar for the posteromedial talocalcaneal ligament, further limiting medial displacement of the astragalus. There is a ridge between the medial and lateral facets for the astragalus, which is very broad in two of the morphospecies. This ridge also forms the medial border of an extremely deep pit which is anteroposteriorly

elongated in some species, bearing the anterior proximal process of the astragalus. This feature is similarly related to stabilising the subtalar ankle joint, imperative not only in locomotion, but also to support the huge bulk of the body when standing erect. This provides an explanation for the reduction of the fifth metatarsal as the majority of the weight is being borne on the medial side of the pes.

The fifth metatarsal is expanded proximally (Adnams-Hodges 1988; Murray 1991, 1995; Wells and Tedford 1995), and may relate to morphological differences of the distal lateral portions of the calcaneum. The entire distolateral portion in the calcaneum is depressed in distal aspect, as well as being angled anteroplantarly, transmitting weight through to the expanded proximal portion of the fifth metatarsal. In four of the sthenurine morphospecies, there is a large transverse plantar sulcus on the plantar surface of the calcaneum, convergent in form with the potoroids.

The tuberous section of the plantar surface provides insertion for the plantar calcaneocuboid ligaments, which tightly bind the calcaneum to the base of the cuboid, fourth and fifth metatarsal. The sthenurine's possession of an elongate transverse plantar sulcus may be related to utilisation of the elastic properties of the ligament originating posteriorly on the calcaneum. As the ligament is not bound to the calcaneum at the plantar sulcus, the ligament may act like a bow across the plantar surface between the calcaneum and the cuboid.

In the sthenurines as with *Macropus rufus* there is evidence for large lateral and medial calcaneocuboid ligaments, suggesting reduced lateral movement. Mobility at the calcaneocuboid articulation is also heavily influenced by the morphology of the distal articulating facets for the cuboid. In two of the morphospecies the dorsolateral facet for the cuboid is particularly narrow, but also broad in three of the morphospecies. The most important functional nature of the calcaneocuboidal step, which is shallow in four of the morphs, suggests the foot may be supinated or pronated at the calcaneocuboid articulation. The dorsolateral facet for the cuboid is also anteroplantarly compressed in a few of the sthenurine groups, convergent in form with *M. rufus*, the distinction being in the degree of truncation of the step. A further consistent feature of the sthenurines is that the dorsomedial and ventromedian facets are fused, surrounding a circular fossa suggesting increased rotational mobility at the calcaneocuboid articulation. The ventromedian facet for the cuboid is much larger in all of the sthenurines than the macropodines. This would be attributed to its weight bearing role during stand-up browsing. In three of the morphospecies, the plantar apex of the ventromedian facet is situated directly below the dorsomedial facet, compared with a more lateral placement of the ventromedian facet, below the calcaneocuboidal step in the other morphospecies. The placement of this fossa indicates where the weight is being borne in the foot, and that, in the former group, the foot was stressed in a slightly pronated position.

Inferred Locomotory and Feeding Habits of the Sthenurines from the Naracoorte Area

On discrete analysis of the sthenurines calcanea, at least eight morphospecies could be identified. The diverse morphology of the calcaneum suggests that they were segregated into a wide range of habitats.

Inferred Habits of Group (1):

There are two morphospecies within this group which were originally thought to represent two sexual morphs of *Sthenurus browneii* (Merilees and Porter 1979). It was not within the scope of this study to include a complete comparison of the sexual dimorphism present in the modern macropodine species, which should be carried out to test such a hypothesis.

It can be inferred from the pes structure that this sthenurine group is adapted mainly for bearing the large weight of the animal during locomotion. The sthenurines in this

group were not able to rotate their feet to the extent of the modern macropodines. Because of the monodactyl nature of the pes, it is concluded that these sthenurines were adapted to a habitat relatively free of obstacles. There are still adaptations apparent to align the foot under the body in the sagittal plane during locomotion.

Inferred Habits of Group (2):

There are three morphospecies in this group. Because the measurements were not able to discriminate to species level, morph 1 of this group has the same relative proportions as the other two. On further examination morph 1 was found to be anatomically very different. There are a number of features discriminating the second two morphs of group (2) which are probably *Sthenurus occidentalis* based on a comparison with a known specimen from the Green-Water Hole at Tantanoola, S.A.:

It can be inferred from the morphology that the pes of this sthenurine group is adapted for bearing the large weight of the animal (approximately 20% greater in mass compared with the largest of the modern macropodine species) during locomotion, and that there are adaptations for greater mobility at the ankle. It would seem that the sthenurines in this group have compensated for the loss of the stabilising lateral digits by having greater ability to control the motion of the foot. The loss of stability at the ankle however would indicate slow locomotion as much of the action of the muscles would be in control of the foot, particularly through uneven terrain. These sthenurines also would have been well adapted for stand-up browsing.

Morph 1 of group (2) shows many adaptations to keeping the pes in line under the body during locomotion, but also show adaptations for being able to rotate the foot internally and externally. These features are most likely related to control of the foot during stand-up browsing, such as moving the digits and the feet, particularly with the feet externally rotated, providing greater stability. The sthenurines of this morphospecies were probably also moderately well adapted to locomotion through habitats with uneven terrain.

Inferred Habits of group (9):

The detailed anatomy of the morphs of group (9) is extremely varied. morph (i) is concluded to be a sexual morph of group (1) morph (ii) with the exception of the comparatively short tuber calcanei. Morph (ii) of group (9), which is surmised to be *Sthenurus gilli*, can be distinguished by the following characters:

The features of morph (ii) of group (9) (tentatively *Sthenurus gilli*) suggest that this species was particularly well adapted to stand-up browsing, being able to externally rotate the foot, producing a stable posture. This species also possessed features allowing the foot to be pronated and supinated. This species had stable upper and lower joint complexes, suggesting that during locomotion the feet were able to be placed underneath the body, possibly through internal rotation of the crus about the articulation with the femur. It is evident that this smaller species does not possess the weight bearing adaptations. This is to be expected considering the small size of this species.

Morph (iii) of group (9) diverges significantly from the general robust form of the remaining sthenurines.

It is evident that this species bears few of the adaptations to locomotion and stand-up browsing recognised in the remainder of the sthenurines. It is proposed that this sthenurine species was particularly gracile and had proficient locomotor capabilities. The depth of the tuber calcanei suggests that the animal still had to bear a substantial weight load, which was subsequently directed primarily in the sagittal plane. There was limited mobility of the foot, extraneous to motion in the sagittal plane. Evidence suggests that during locomotion, the feet did not have to be forced underneath the body to support a great weight. It is concluded that this species was adapted to a plains environment, and was the most gracile or slender of the sthenurines. This sthenurine species was not particularly well adapted to stand-up browsing.

CONCLUSIONS

The shared pedal characters of the diprotodont marsupials were compared with other diprotodont marsupials including the possum, wombat and koala. Using these as an outgroup, the musky rat-kangaroo, *Hypsiprymnodon* was shown to possess the fewest derived characters of the macropodids. The western grey kangaroo, *Macropus fuligi-nosus* was shown to be very derived relative to the condition expressed in *Hypsiprymnodon*.

A study of the functional anatomy of the hindlimb and pes of *Macropus fuliginosus* demonstrated that the derived morphology related directly to its specialised bipedal mode of locomotion. Some of the macropodines have diverged, and are present in varied habi-tats. *Dendrolagus bennettianus*, the tree-dwelling kangaroo, possessed a short broad pes, and an ankle structure with high mobility, clearly adaptations to an arboreal habitat. *Macropus rufus*, the plains-dwelling kangaroo showed adaptations such as a narrow elongated pes with a highly constrained ankle, which relate to locomotion in the even ter-rain plains habitats.

A cluster analysis of the fossil calcanea sorted the sthenurines from the macrop-odines. The sthenurines could further be broken down into nine distinct morphological groups, some of which could be assigned to particular species.

The main features uniting the sthenurines suggest that the sthenurine pes was adapted for stand-up browsing. While there is no doubt that like the modern kangaroos, the sthenurines utilised the bipedal hop for locomotion, the results support earlier find-ings that their morphology suggests that the feet were adapted to bearing the great weight of the animal during locomotion.

However, some of the sthenurine calcanea, while still possessing adaptations for stand-up browsing were noted to be particularly slender, and lacked the adaptations relat-ed to weight bearing. Evidence suggests that the sthenurines from the Naracoorte area were partitioned into several different habitats, from scrub and uneven terrain to plains environments.

The distinct morphological variance exhibited in the characters of the pes of these sthenurine forms suggest it may be possible to reconstruct the phylogeny of these groups based on anatomy of the foot.

AKNOWLEDGEMENTS

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